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Phase Shift of a Tidal Rhythm by Light-Dark Cycles in the Semi-Terrestrial Crab *Sesarma pictum*

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Abstract. The larval release activity of the semi-terrestrial crab *Sesarma pictum* was monitored for three-week periods under laboratory conditions of constant and cyclic light. Under conditions of constant dim light, the rhythm for the first ten days was unimodal (larval release just after the nocturnal high tide) and then became bimodal (no apparent synchrony with the tides or with other members of the population) for the remainder of the experimental period. On the other hand, in photoperiods similar to those in the field, the rhythm was maintained; the phase was bimodal and the timing of larval release was delayed 1–2 h from the predicted times of high water in the habitat. When the photoperiod was advanced or delayed, the tidal rhythm was phase-shifted accordingly. The photoperiod does entrain the release rhythm to bimodal tidal cycle. So the phase-shift of a tidal rhythm by 24-h LD cycles is a very difficult phenomenon to explain.

Introduction

In their natural habitats, intertidal and estuarine animals are exposed, not only to the day-night cycle (24 h), but also to the rhythmic ebb and flow of the tides, which include 12.4-h, 24.8-h, and 15-day components. Having adapted to such an environment, marine organisms often show a complex activity pattern with circadian, circatidal, and circa-semilunar frequencies; the dominant rhythmicity is circadian in some species, and circatidal or semilunar in others (see reviews by Neumann, 1981; DeCoursey, 1983).

Compared with the terrestrial animals, information about the biological timing systems is relatively limited in marine animals. This paucity of information is partly due to the complexity of environmental cycles. In addition, most biological timings have been investigated in locomotor activities. The noisy nature of these activities, and the individual variability in the responses to environmental cycles, have made the analyses difficult in most aquatic animals. For example, when the locomotor activity of the fiddler crab *Uca crenulata* was monitored in constant light or 24-h light-dark conditions, half of the experimental crabs only showed a rhythmic activity; the activity of the remaining half was random (Honegger, 1973).

Clearly demarcated biological rhythms have been reported in the swimming activity of some marine crustaceans (Enright, 1963, 1972). The records of their activity have demonstrated predominantly circatidal rhythms that were not affected by light-dark cycles in the laboratory. Animals do entrain or respond to simulated tidal stimuli, such as wave action in the isopod *Excirolana* (Enright, 1965), or cycles of hydrostatic pressure in the amphipods *Synchelidium* (Enright, 1962) and *Corophium* (Morgan, 1965).

Precise biological timings also often develop in reproductive phenomena, and this has been observed in a variety of marine animals, including the polychaete *Platynereis* (Hauenschild, 1960), the intertidal midge *Clunio* (Hashimoto, 1976; Neumann, 1976), and many species of Crustacea (Branford, 1978; DeCoursey, 1979, 1983). The larval release behavior of the estuarine terrestrial crab *Sesarma haematocheir* is also synchronized with environmental light and tidal cycles, showing a unimodal tidal rhythm that coincides with the times of nocturnal high water (Saigusa, 1982, 1985). A phase jump is involved in the timing process, so that this tidal rhythm appears at 15-day intervals. Experimental analyses indicated that the timing is endogenously controlled, and that the phase of the rhythm can be shifted by artificial 24-h light-dark (LD) cycles (Saigusa, 1986). An important problem is the timing mechanism underlying the tide-synchronized biological rhythm, the phase of which is shifted by day-night cycles.

In this paper, ovigerous females of *Sesarma pictum* were used for experiments, because larval release activity in

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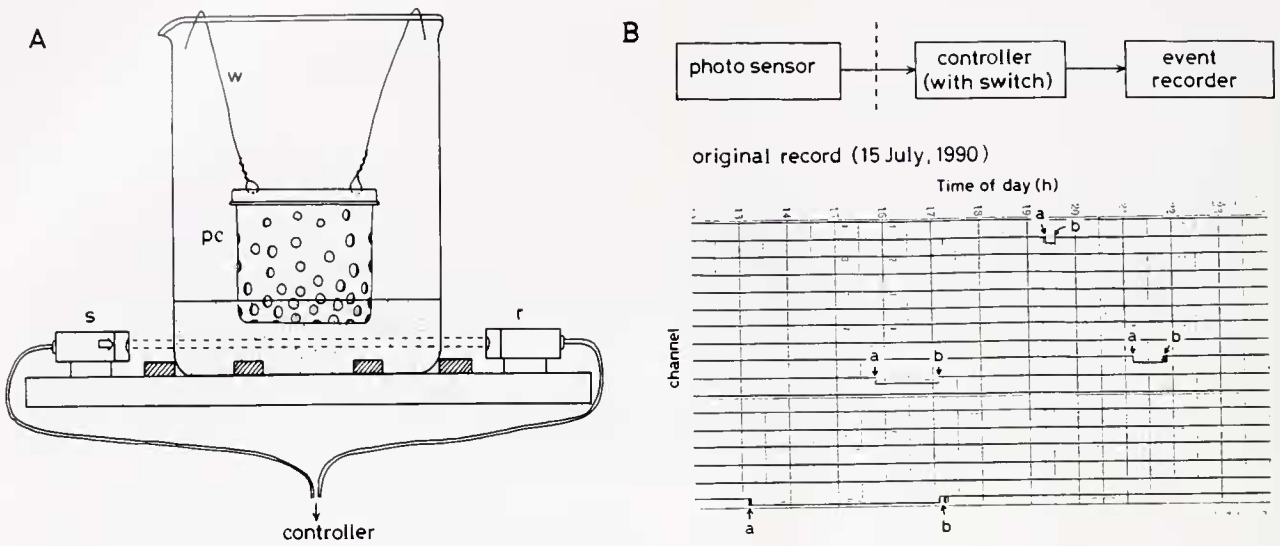

Figure 1. System for recording the larval release activity of *Sesarma pictum* females. A. The apparatus used to detect the time of day of larval release. w: fine wire. pc: plastic cage to confine an ovigerous crab. s and r: infrared source and receiver (E3S-2E4, Omron Co. Ltd., Japan). The glass beaker illustrated here is the larger one (13.5 cm diameter; see text). B. An example of an original record showing 4 out of 17 females releasing their larvae (a part of the data illustrated in Figure 2). The output of the sensor unit was monitored by an event recorder (R17-H12T, Fuji Electric Co. Ltd., Japan) through a controller (S3S-A-10, Omron). a: time of larval release by a female. b: time when that female was removed from the experimental chamber with her beaker. Simultaneously, a new beaker with a plastic cage that confined another ovigerous female was placed in each apparatus.

this species has a tidal rhythm with a bimodal phase (12.5-h period) that has no apparent circadian component. The present paper asks whether this tidal rhythm is also affected by the day-night cycle, and it discusses possible mechanisms for this influence.

Materials and Methods

Sesarma pictum inhabits banks above the water's edge in the intertidal zone. Male and female crabs spend the winter hibernating in burrows dug into the bank, but they become active in the latter half of April. In early summer (June–July), the females incubate their eggs in their folded abdomens, where the embryos are ventilated by movements of the pleopods. When embryonic development is completed, the females enter the water to liberate their zoea larvae. The larval release behavior has not been observed in the field because it is not carried out at the water's edge, as is that of *S. haematocheir* (Saigusa, 1982, 1985). Rather, the ovigerous females of *S. pictum* enter the water at about high tide, and then soon disappear in the depths; possibly they release their larvae in the water near the shore.

Ovigerous females were collected from the seacoast at Kasaoka, Okayama Prefecture. The crabs occur in narrow crevices between rocks on the bank; they were stimulated to emerge with a thin stick, and were then captured by hand. Once suitable numbers had been collected, they were brought into the laboratory and placed in aquaria (70 cm long, 40 cm wide, and 25 cm high). The aquaria had a shallow pool of diluted seawater (salinity at about 20‰) at the bottom, and hiding places (moistened with fresh water) made of boards set above the surface of water. The crabs were fed every few days. The experimental rooms were equipped with controlled light and temperature. Temperature was at 23 ± 1.5°C; luminous intensity was about 700–1200 lux at the floor with the light on, and less than 0.01 lux in the dark phase. Only two experiments were carried out under continuous light, and in these cases the luminous intensity was at 0.5–1.0 lux, or 100–300 lux, respectively.

The eggs (*i.e.*, embryos with egg capsules) of each female were checked by eye every day, and those crabs carrying embryos that seemed likely to hatch within a few days were individually set in a recording apparatus placed in the same room (Fig. 1A). With this apparatus, the time of larval release could be monitored without any change in the ambient lighting conditions. The day of hatching is difficult to predict; the only indication that hatching is imminent is the brownish green color of the embryos (mainly caused by yolk consumption). The larval release behavior of *S. pictum* was observed in the laboratory, and was generally not as vigorous as that of *S. haematocheir*. The female repeatedly flexed her abdomen inward and made associated movements of the pleopods bearing embryos. These pumping

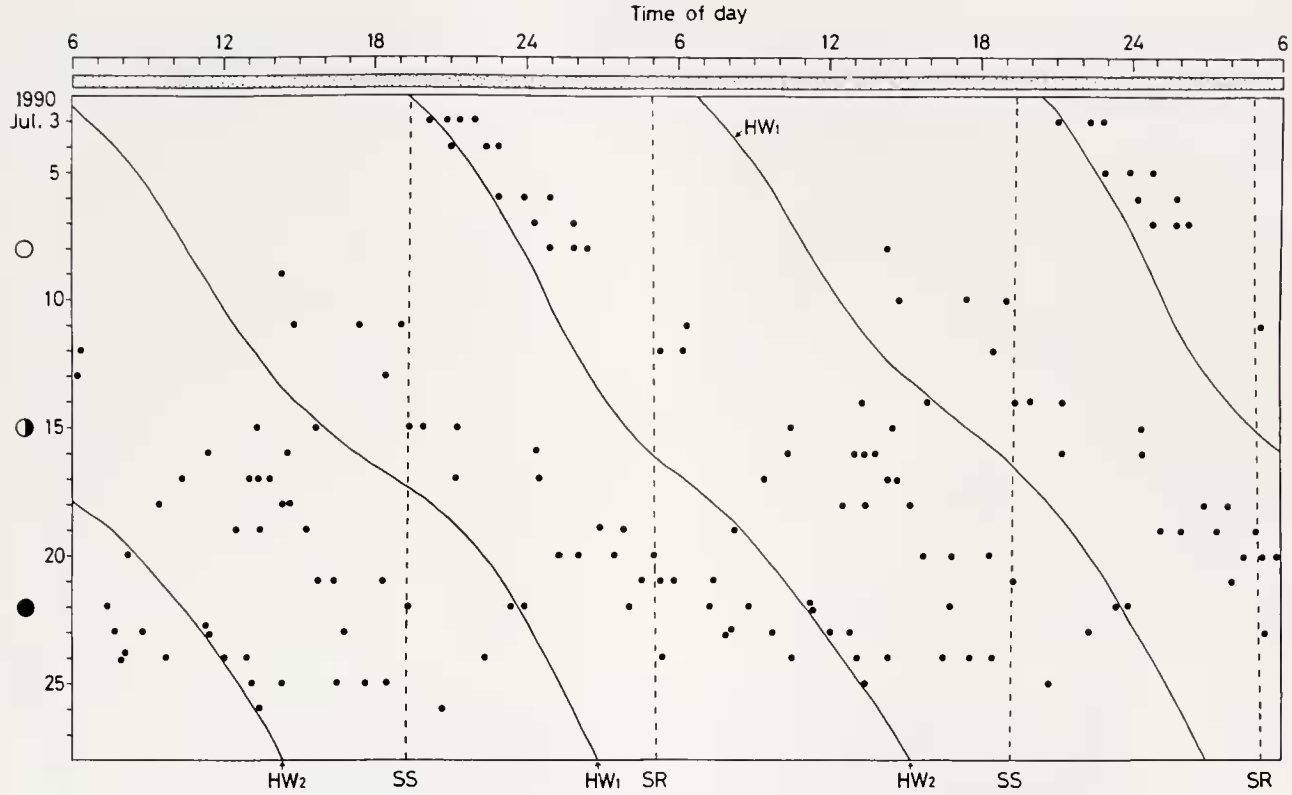

Figure 2. Time of day of larval release monitored under a regime of continuous light (LL: 0.5–1.0 lux) and no tidal influence in the laboratory. All of the ovigerous females were collected in the field on 3 July 1990; black dots indicate the time of day of larval release by those females. For comparison, environmental cycles in the field are characterized by the times of sunset (SS) and sunrise (SR), by the curves connecting predicted time of day of high tides (HW_1 and HW_2), and by the phase of the moon (○: full moon, ◑: the last quarter of the moon, ●: new moon). The entire record is duplicated on the right and displaced upwards one day, so that each day's data can be matched with those of the following day. Eighty (80) females were used in this experiment.

movements swept clouds of newly hatched zoeae away from the female.

The larval release recording system consisted of a sensor unit (infrared source and receiver) placed inside the experimental room, and a controller unit placed outside. Each ovigerous female was confined in a separate, small plastic cage (6 cm in diameter and 8 cm in height) with many holes drilled in the bottom and sides. As Figure 1A shows, the cage was suspended by a fine wire from the rim of a glass beaker containing diluted, clean seawater (salinity at about 20‰). The experimental procedures for monitoring the larval release activity of *S. pictum* were basically the same as those for *S. haematocheir* (Fig. 1B), and they have already been described elsewhere (Saigusa, 1986).

For each female, one of two kinds of glass beakers was selected to hold her plastic cage: a bigger one (13.5 cm in diameter), or a smaller one (11 cm in diameter). The selection was made to ensure that the photoelectric switch would respond and was based on the size of the egg sponge carried by the female. Moreover, because the ovigerous female of *S. pictum* has a smaller carapace (1.6–2.5 cm) than *S. haematocheir,* the amount of seawater in the larger beaker was reduced to 0.5 l, and to 0.3–0.4 l in the smaller one. The number of ovigerous females used in each experiment is described in the figure legends or in the text. (Some females were released into the aquaria before being confined to cages. Because the time of the release of those females was not monitored, such releases were not included in the figures.) The animals were not fed after they had been confined in the recording apparatus.

Results

The females used in the present experiments were randomly collected from the field; thus, some crabs seemed ready to release larvae within a few days, whereas others carried eggs that seemed to have commenced incubation just one or two days before. The larval release by these females was completed within three weeks after the collection, suggesting that females incubate their embryos for about 2–3 weeks.

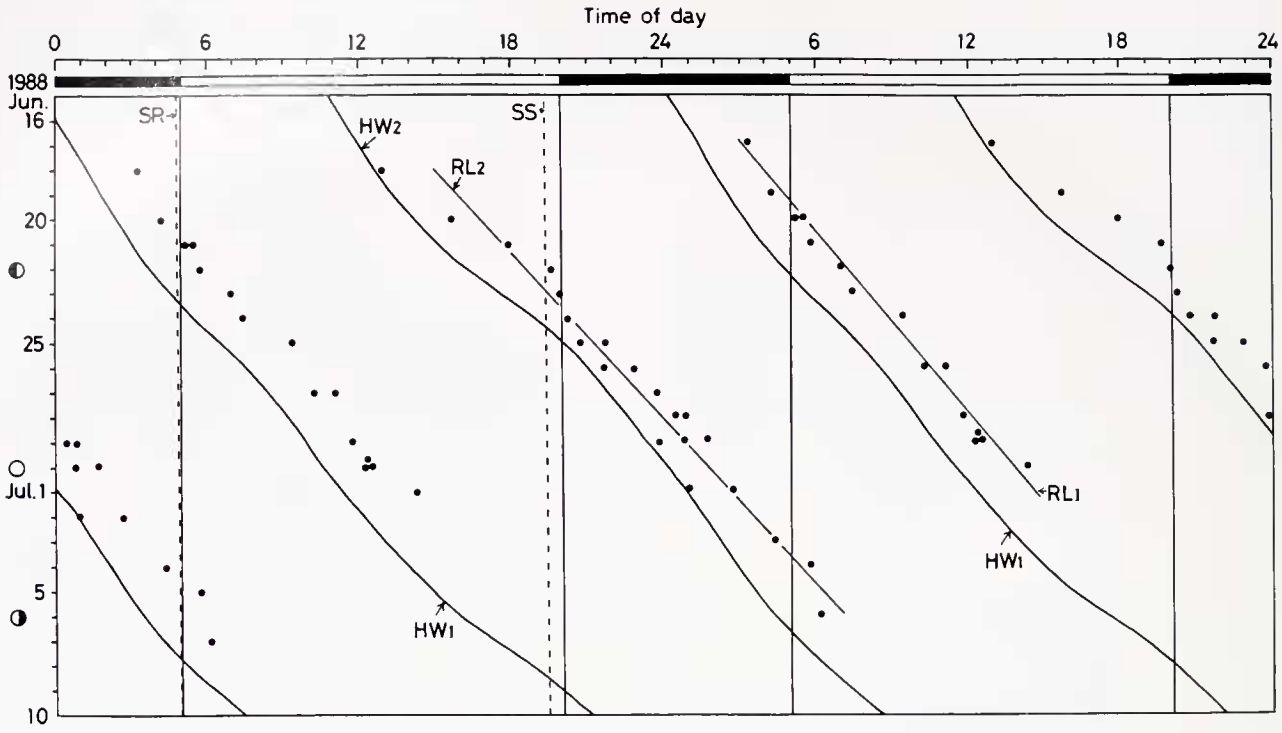

Figure 3. Daily timing of larval release by *Sesarma pictum* monitored under the conditions of a 24-h light-dark (LD) cycle in the laboratory. Forty crabs were used. Date of collection: 16 June 1988. Vertical lines indicate the times of light-off and light-on in the chamber, respectively. SS and SR are the times of sunset and sunrise in nature. Diagonal curves (HW_1 and HW_2) connect the times of high water in the field. Diagonal lines (RL_1 and RL_2) are least squares regression lines fitted to each phase of the tidal rhythm. The period length of each phase (τ) is estimated from the slope (a) of its regression line (τ = 24h + a). The slopes of RL_1 and RL_2 are 0.75 and 0.84, respectively. The regression lines are based on those data obtained after the phase shift was considered to have been completed.

The first experiment was designed to determine whether an endogenous component is involved in the larval release activity and, if so, whether this component corresponds to the day-night cycle or to tidal cycle at the local habitat. For these purposes, the larval release activity of the population (80 specimens) was monitored under constant, very dim light (LL) conditions for more than three weeks following collection. As indicated in Figure 2, the larval release activity persisted under these conditions. For the first 10 days, the phase of the rhythm was unimdal (24.5-h period) and the larval release roughly coincided with the nocturnal high tides. The release rhythm then became bimodal (12.5-h period), but no apparent synchrony with the tides, or with other members of the population, appeared for the remainder of the experimental period. A similar experiment, with 40 individuals under stronger luminous intensity (100–300 lux), also had the same tendency (not illustrated).

To examine the effect of light regime, experiments were then conducted with a 15-h light: 9-h dark photoperiod; *i.e.*, the phase of the cycle was set to be similar to that in the field. The effects of cyclic light were markedly different from those illustrated in Figure 2: the timing of the larval release was closely correlated with the tidal cycles (high water) for at least three weeks (Fig. 3). The phase of this rhythm is clearly bimodal (12.5-h period). Least squares regression lines fitted to each phase of the rhythm (RL_1 and RL_2) showed that the timing of release monitored in the laboratory was delayed 1–2 h from the predicted times of high water in the habitat. The correlation of larval release with the tidal cycle in the habitat of the crabs continued throughout the experiment. Another experiment, with 50 females and the same light conditions, was performed on 1–20 July 1987; the results were the same as those of Figure 3 (not illustrated). A comparison of Figures 2 and 3 suggests that a 24-h natural light-dark cycle maintains the normal tidal phase of a population rhythm.

Next, I examined whether the phase of the tidal rhythm can be affected if the phase of the experimental cyclic light is shifted from the natural day-night cycles. The following experiments were made to confirm this point quantitatively. In Figure 4, the phase of the artificial day-night cycle was advanced relative to the natural light cycle, by 6.25 h at lights-on, and by 7 h at lights-off. After some days had elapsed, the time of release shifted ahead of the predicted high water curves. This suggests an advanced

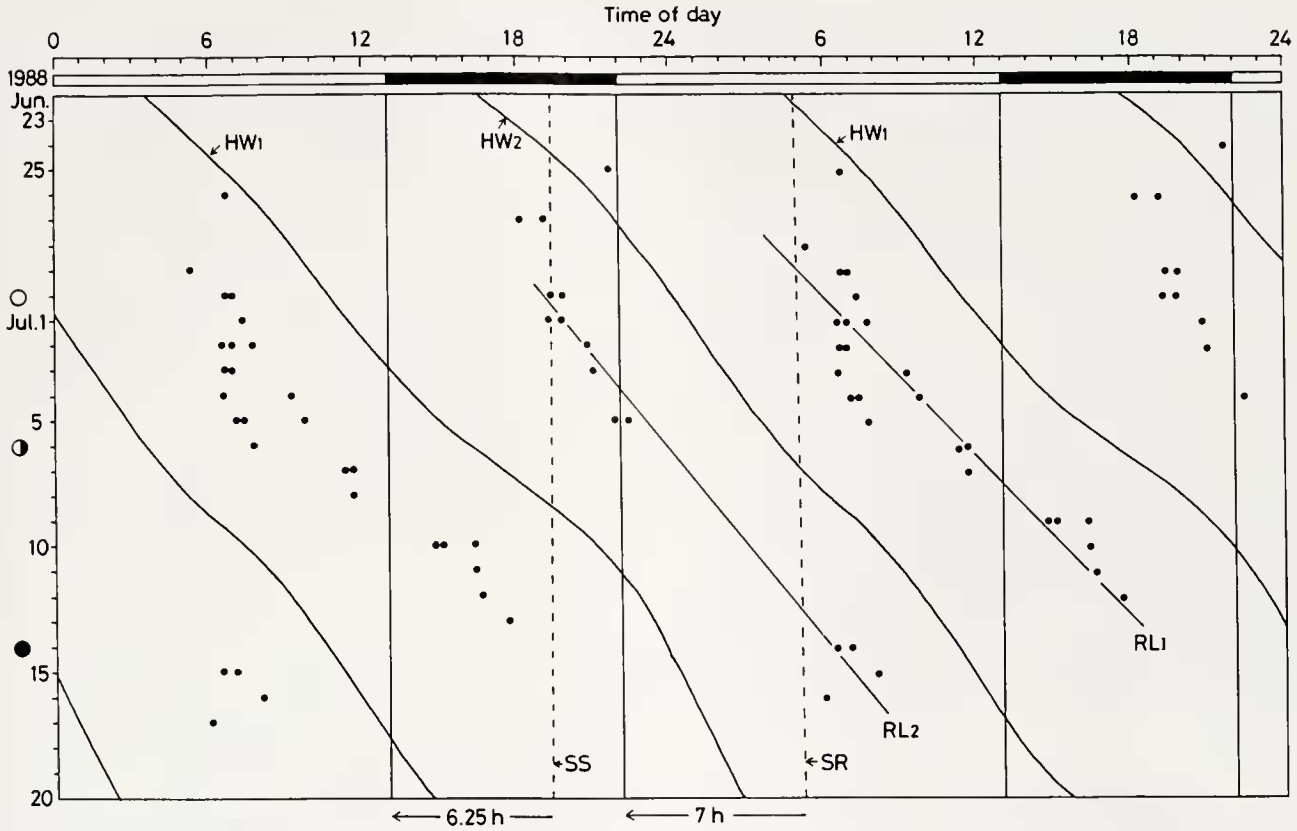

Figure 4. Time of day of larval release monitored under a 24-h light-dark regime (LD 15:9), the phase of which was *changed* by 6–7 h with respect to the natural conditions. Times of light-off and light-on in the artificial light cycles are shown by vertical lines (light-on at 22:00, light-off at 13:00), and times of sunset and sunrise are marked by the broken lines. RL_1 and RL_2 indicate least squares regression lines applied to the new phase after the shift; *i.e.*, the data from 29 June–13 July for RL_1, and those of 30 June–17 July for RL_2. Other symbols are the same as in Figure 2. Collection of crabs: 23 June 1988. The slopes of RL_1 and RL_2 are 0.76 and 0.80, respectively. Fifty animals were used in the experiment.

phase-shift. The magnitude of the shifts in the two phases were somewhat different; *i.e.*, whereas the time difference between HW_1 and RL_1 was 5–6 h, that between HW_2 and RL_2 was 4–5 h. The phase differences between the rhythms in both Figures 2 and 3, corresponded to the time lag between the natural day-night and the artificial 24-h LD cycles.

Another experiment was also meant to verify that the magnitude of the phase-shift of the tidal rhythm is dependent on the phase difference between natural and artificial day-night cycles. In this case, the experiment asked whether the phase can be delayed. One hundred females were used in these experiments, and the light regime was shifted by 5 h at lights-on and by 5.7 h at lights-off. In this experiment, the data suggest that, after about 10 days, a delayed phase-shift occurred (Fig. 5). Another experiment, in which 35 animals received the same treatment (23 July to 7 August 1987), clearly demonstrated a similar phase delay (not illustrated). Figure 5 also shows that the phase of the population rhythm remained stable with respect to the phase of high water, for at least the next 2–3 weeks, with no notable desynchronization of the individuals. The time lag between HW_1 and RL_1 was 5.5–7 h, and between HW_2 and RL_2 it was 5.5–6.5 h. The duration of the phase delay could not be determined in these experiments, because the number of the females incubating the next clutch diminished.

The experiments described above were performed with crabs collected on different dates. Uncertainties remained, therefore, about whether a light cycle can actually phase-shift a tidal rhythm, and if so, whether advancing or delaying the photoperiod truly corresponds to the change in the tidal rhythm. To meet this question, about 200 ovigerous females were collected from the field on 3–4 July 1991, and randomly separated in the laboratory into two groups of similar size. One group was exposed to an artificial 24-h LD cycle, the phase of which was similar to the natural LD cycle (Fig. 6A); the other group was exposed to an artificial LD cycle that was advanced 4–5 h from the natural light cycle (Fig. 6B).

In the control experiment (Fig. 6A), the larval release occurred just after the time of high tides in the field. The

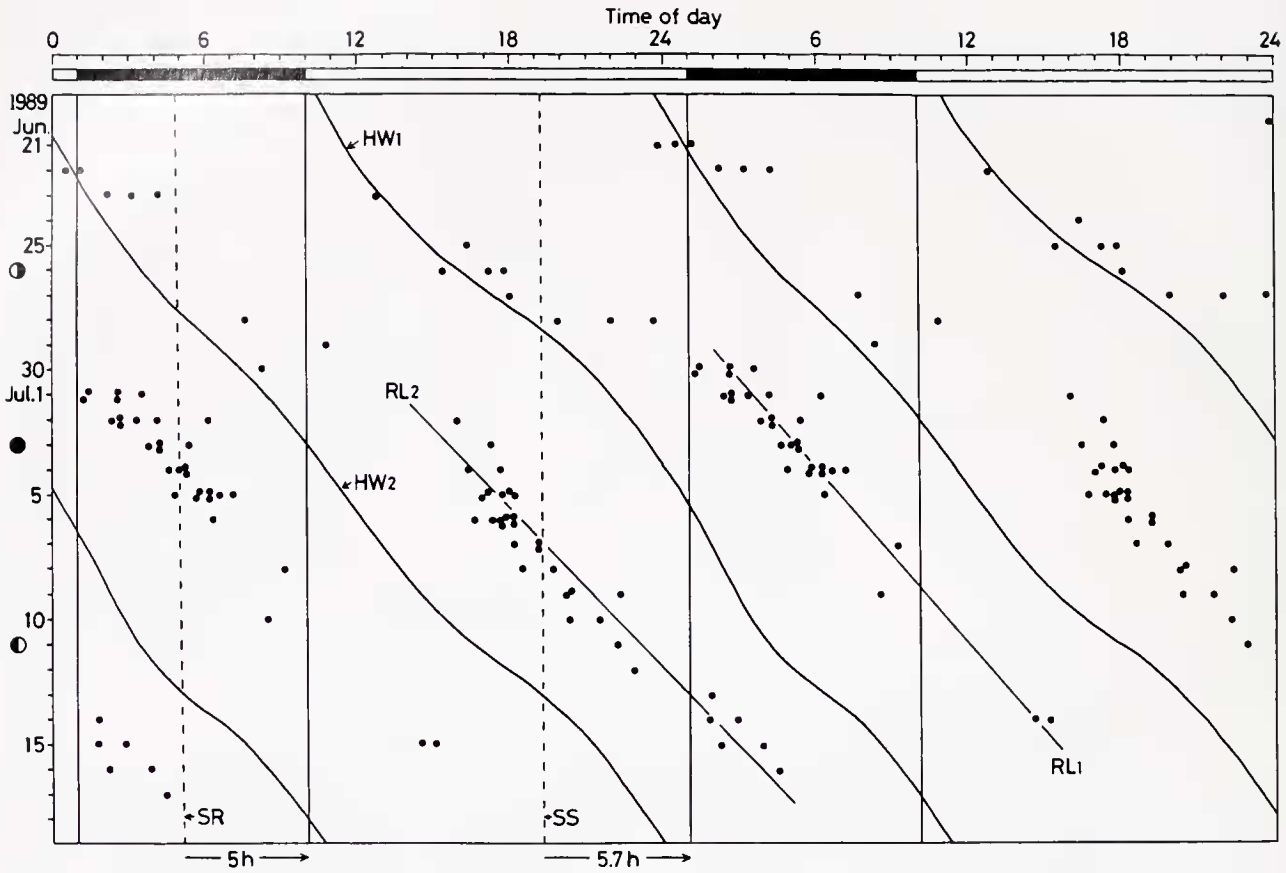

Figure 5. Time of day of larval release monitored under a 24-h light-dark regime (LD 15:9), the phase of which was *delayed* by 5–6 h from the natural light cycle. Times of light-on and light-off were 1:00 and 10:00, respectively. All of the crabs were collected on 21 June 1989. Some of the females incubated a second clutch in the laboratory, and the larval release activity of those crabs was also monitored. The estimated slope of RL_1 and RL_2 is 0.85 and 0.86, respectively. ◑: the last quarter of the moon, ●: new moon, ◐: the first quarter. About 100 females were used in the experiment.

phase of this rhythm was clearly bimodal. These features were the same as those in Figure 3. The crabs exposed to the light cycle that had been advanced (Fig. 6B) also showed a bimodal tidal rhythm, but a week had elapsed, and the time of release shifted ahead of the time of high tides. The time lag between the activity after 10 July and high tide (HW_2) showed an advancing phase-shift of about 4 h.

No clear indication of a semilunar component (*i.e.*, a semi-monthly fluctuation in the number of females releasing larvae per day) was found in these results. Neither was a 24-h solar day (*i.e.*, circadian) component detected, at least in the activity pattern itself.

Discussion

The purpose of devising experiments in constant light (*e.g.*, Fig. 2) is to demonstrate a free-running rhythm. Certainly the larval release was roughly correlated with the time of nocturnal high tides for the first 10 days, and then the rhythm became bimodal. However, no apparent synchrony with the tides, or other individuals in the population, was seen for the latter half of the experimental period; so no free-running rhythm was clearly evident in Figure 2.

In most studies of rhythmic behavior, activities that are carried out repeatedly by each individual are monitored throughout the investigation. In this work, however, each crab released larvae just once during a three-week experimental period; so no free-running rhythm was evident. A possible explanation of the data in Figure 2 is, therefore, that the constant light increased the variability of the free-running period in each individual, desynchronizing the population rhythm.

The first question arising here is related to the environmental cues that entrain the tidal rhythm of this species. Circa-tidal rhythms are known to respond to stimuli correlated with on-shore tides, and not to day-night cycles. Enright (1965) showed that cycles of water turbulence can effectively entrain the circa-tidal rhythm of the isopod

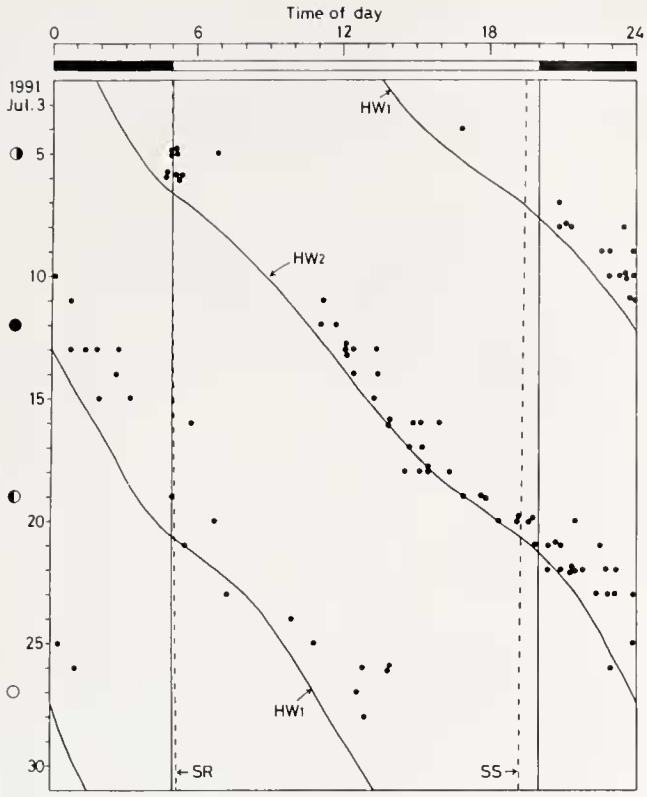

Figure 6A. Time of day of larval release monitored under a 24-h LD cycle (LD 15:9), the phase of which was *similar* to that of the field. Date of collection: 3–4 July 1991. About 100 animals were used in the experiment. Symbols were the same as in Figure 2.

Excirolana. Cyclical or non-cyclical changes of hydrostatic pressure have been shown to cause behavioral responses in the amphipods (Enright, 1962; Morgan, 1965). However, all the experimental data obtained in this study (Figs. 2–5 and 6A, B) have demonstrated that a light regime actually takes part in the phase shift. The 24-h LD cycle may be the zeitgeber of the *Sesarma pictum* tidal rhythm. In the field, however, this rhythm is not likely to be entrained solely by the 24-h LD cycle.

The tidal rhythm of *Sesarma haematocheir* was entrained by 24.5-h artificial moonlight cycles administered in the dark period of a 24-h LD cycle (Saigusa, 1988, 1989). In view of these studies, the *S. pictum* larval release rhythm could be entrained by more than one environmental cue. A 24-h LD cycle is one zeitgeber, but others remain unknown. The habitat of *S. pictum* is restricted to the bank along the shoreline, so tidally correlated factors, such as the periodic fluctuations of water turbulence on the shore, should also be considered.

The second, and central, question posed in this paper is the effect of light on the tidal rhythm of *S. pictum*. If the results of Figures 4 and 5, and those of Figure 2, were regarded as arising from substantially similar mechanisms, there would be no need to assume a phase shift caused by the environmental light cycle. In this case, one possible explanation is that light cycles exert some superficial influence on the phase of the tidal rhythm irrespective of timing mechanisms, causing abnormal phasing of the rhythm. However, the results of Figure 6A and B would completely deny such a possibility; a photoperiod does entrain larval release rhythm to a bimodal tidal cycle. Because a 24-h LD cycle can evoke a phase shift of the tidal rhythm, then the difficulty is understanding the timing mechanism involved.

Many investigators have found that behavioral and physiological events in marine organisms not only coincide with the tidal cycle, but are also correlated with the day-night cycle to produce activity patterns with simultaneous daily and tidal components (Naylor, 1958; Barnwell, 1966; Palmer and Round, 1967; Honegger, 1973; Benson and Lewis, 1976). Accordingly, recent interpretations have included two types of internal clocks: one of circatidal frequency, and the other of circadian frequency (Naylor, 1958; Barnwell, 1966, 1968; Palmer and Round, 1967; Benson and Lewis, 1976; Webb, 1976). For example, two internal clocks were proposed to explain noc-

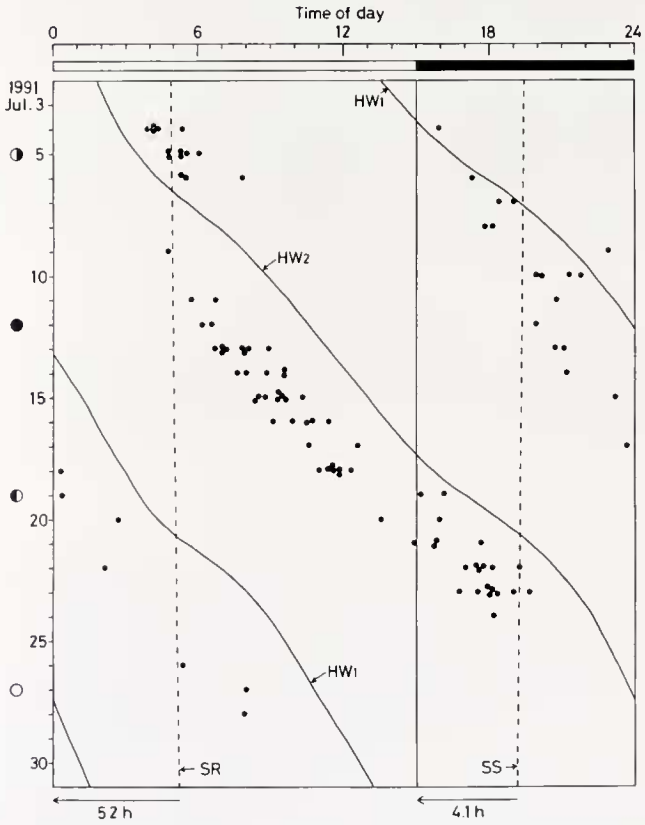

Figure 6B. Time of day of larval release recorded in a 24-h LD cycle (LD 15:9), the phase of which was *advanced* by 4–5 h from that of the field. Date of collection was the same as in Figure 6A. Times of light-on and light-off were at 0:00 and 15:00, respectively. One hundred and five animals were used in the experiment.

turnal locomotion in the amphipod *Talorchestia* (Benson and Lewis, 1976). One of these, a circadian clock, controls the nocturnal phase of the activity, and the other, a circa-tidal clock, inhibits the activity around the time of nocturnal high water.

The phenomenon reported in this paper, *i.e.*, phase shift of the tidal rhythm appearing under cyclic light (Figs. 4, 5, and 6B), could not be explained in terms of an interaction between circa-tidal and hidden circadian rhythms operating simultaneously within individuals. The reason is based on the understanding that a circa-tidal rhythm is only the expression of a circadian rhythm which, as a result of an adaptation to marine environment, has slightly modified its internal period and is responsible to tide-correlated zeitgebers, too. Yet clearly, the circa-tidal rhythm of *S. pictum* cannot be explained in terms of a hypothesis requiring that those tide-correlated zeitgebers affect a circadian (bimodal) rhythm directly, changing its internal period to that of a bimodal tidal cycle.

The nocturnal release rhythm of *S. haematocheir* was, therefore, accounted for by a hypothesis similar to the mechanisms proposed by Pittendrigh and coworkers (Pittendrigh, 1960, 1981; Pittendrigh and Bruce, 1959) (see Saigusa, 1986 and 1988, for details). In that model, when the driven oscillator is delayed until dawn, it leaps back to dusk. However, if one wants to explain the effect of light by the mechanism that was applied to *S. haematocheir*, then one would have to assume that the driving oscillator can control the phase of the driven oscillator which has a different period. Perhaps such an assumption is not realistic. Thus, the phase-shift of a tidal rhythm by 24-h LD cycle is a very difficult phenomenon to explain.

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